

NEW MIOCENE LEAF-NOSED BATS (MICROCHIROPTERA: HIPPOSIDERIDAE) FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

SUZANNE HAND

Hand, S.J. 1997 06 30: New Miocene leaf-nosed bats (Microchiroptera: Hipposideridae) from Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 335-349. Brisbane. ISSN 0079-8835.

Two new Australian Tertiary hipposiderids are described on the basis of skull and dental material recovered from Bitesantennary Site, a Miocene cave-fill on the Site D Plateau, Riversleigh, northwestern Queensland. The new species are closely related to *Hipposideros* (*Brachhipposideros*) *nooraleebus* Sigé, Hand & Archer from Riversleigh's Microsite, and the living northern Australian *Rhinonictoris aurantius* (Gray). One species is referred to *Rhinonictoris*, the other tentatively referred to *Brachhipposideros*. The subgenus *Brachhipposideros* Sigé is raised to generic rank to better reflect relationships of its species.
□ *Miocene, Riversleigh, hipposiderids, leaf-nosed bats.*

Suzanne J. Hand, School of Biological Science, University of New South Wales, New South Wales 2052, Australia; received 4 December 1996.

Bitesantennary Site, in early Miocene (Archer et al., 1989; Creaser, 1997) freshwater limestone on the NE edge of the Site D Plateau at Riversleigh (Hand et al., 1989; Archer et al., 1989, 1994) covers approximately 150m² and contains thousands of bat skulls, limb bones and snails. Almost all are complete, suggesting fossilisation at or very near the point of accumulation. This deposit is interpreted as a cave-fill (Hand et al., 1989) and contains at least 11 microchiropteran species - 10 hipposiderids and a megadermatid. At least 4 of the Bitesantennary hipposiderids are known from many hundreds of partial and complete skulls. Two of the hipposiderids, which are morphologically similar to Microsite's *Brachhipposideros nooraleebus* Sigé et al., 1982, are described and their phylogenetic relationships and palaeoecology are discussed.

Skull terminology follows Hand (1993, 1995); dental terminology follows Sigé et al. (1982). Stratigraphic nomenclature for the Riversleigh region follows Archer et al. (1989, 1994; Creaser this volume). The prefix QMF refers to specimens held in the fossil collections of the Queensland Museum, Brisbane.

SYSTEMATICS

Suborder MICROCHIROPTERA Dobson, 1875
Superfamily RHINOLOPHOIDEA Weber,
1928
Family HIPPOSIDERIDAE Miller, 1907

Rhinonictoris Gray, 1847

Rhinonictoris tedfordi sp. nov. (Figs 1-2, Table 1)

MATERIAL. Holotype QMF22910, partial skull with RM², LM². Paratypes QMF22911, partial skull with RP¹-M¹ and LM²⁻³; QMF22912, maxillary fragment with RC¹-M¹, QMF22840, rostrum with LC¹-M¹; types from early Miocene (System B) Bitesantennary Site. Other material: Bitesantennary Site: QMF22831, QMF22841, QMF22842, QMF22845, QMF22854, QMF22859, QMF22865, QMF22871, QMF22890, QMF22891, QMF22893, QMF22909. White Hunter Site (System A): QMF22921, QMF22922. RV Site (System B): QMF22930, QMF22931, QMF22932, QMF22913. Upper Site (System B): QMF22914. White Hunter, RV and Upper Sites are about 2km SSW of the type locality.

ETYMOLOGY. For Richard Tedford, American Museum of Natural History who described the first Tertiary mammals from Riversleigh in 1967.

ASSOCIATED FAUNA AND TAPHONOMY. The cave-fill (Hand et al., 1989) at the type locality contains thousands of well preserved, almost complete bat skulls and limb bones, suggesting fossilisation at or near the point of accumulation. Contact between the fill and older cave wall have been identified. The deposit's many freshwater snails suggest that the depositional area was open to light and under water for some period during its history. A travertine floor, including a large stalagmite, has been found at the base of the deposit.

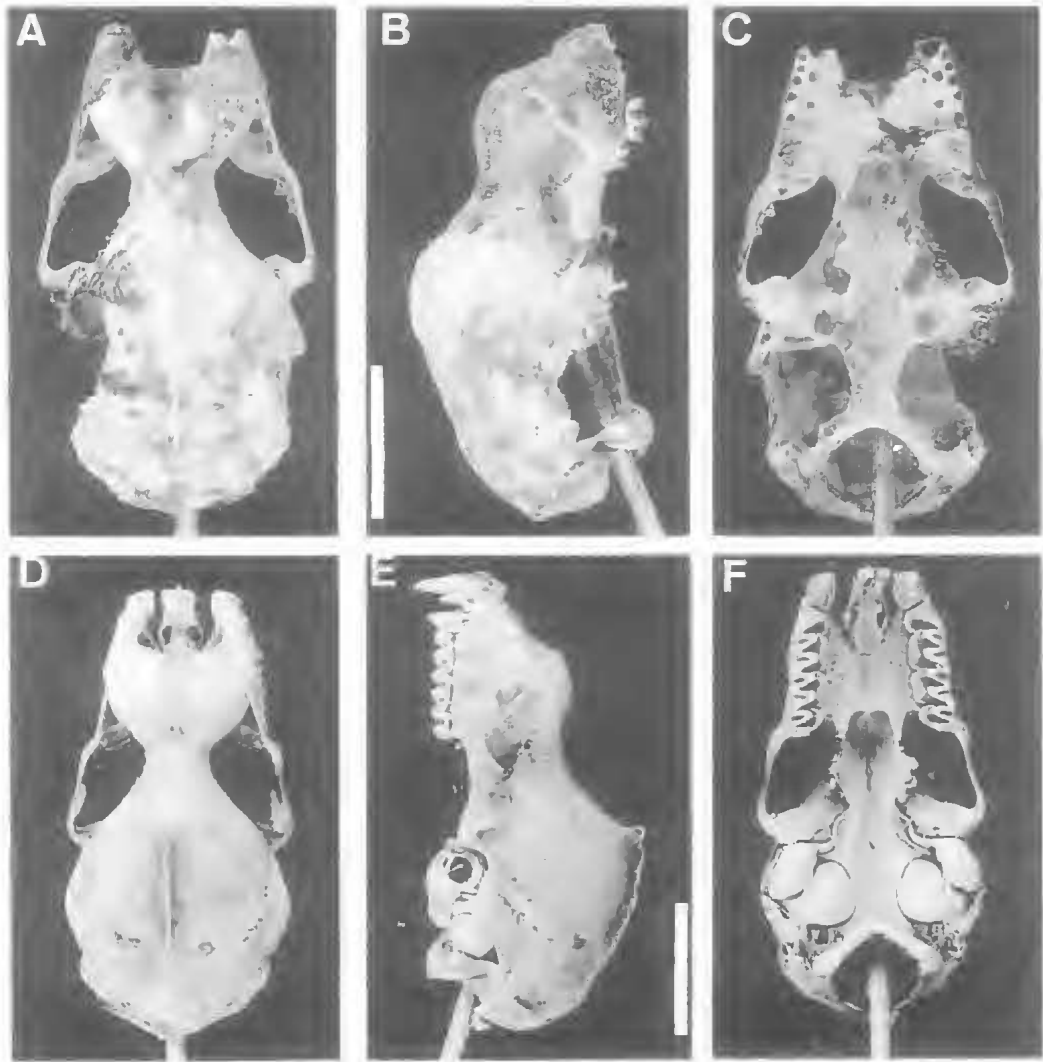


FIG. 1. A-C, *Rhinonictes tedfordi* sp. nov., QMF22910, holotype, from Bitesantennary Site, Riversleigh, northwestern Queensland. A, dorsal view; B, lateral view; C, ventral view. D-F, *Rhinonictes aurantius*, AR 15400, Klondyke Queens Mine, Marble Bar, Western Australia. D, dorsal view; E, lateral view; F, ventral view. Scale indicates 5 mm.

Bitesantennary Site contains *R. tedfordi*, ?*B. watsoni* and at least 8 other hipposiderids and a megadermatid with rarer frogs, lizards, a boid, a stork, swift, peramelids, a dasyurid and a bulungamayine macropodid (Archer et al., 1994).

In the complex lacustrine White Hunter, Upper and RV deposits the vertebrate faunas are much more diverse, with the Upper Local Fauna (Archer et al. 1994) one of Riversleigh's richest.

DESCRIPTION. In comparison to Miocene *B.*

nooraleebns Sigé et al., 1982 and Recent *Rhinonictes aurantius* (Gray, 1845).

Skull 10-20% smaller than *R. aurantius* and approximately same size as *B. nooraleebns* (braincase may be slightly longer in *R. tedfordi*). Proportions similar to *B. nooraleebns*: rostrum wide and long with respect to braincase, approximately 2/3 braincase length, 2/3 maximum (mastoid) width and twice interorbital width. Zygomatic width greater than mastoid width. Maximum height of the skull dorsal to the glenoid process as in *R. aurantius*. In dorsal view, poste-

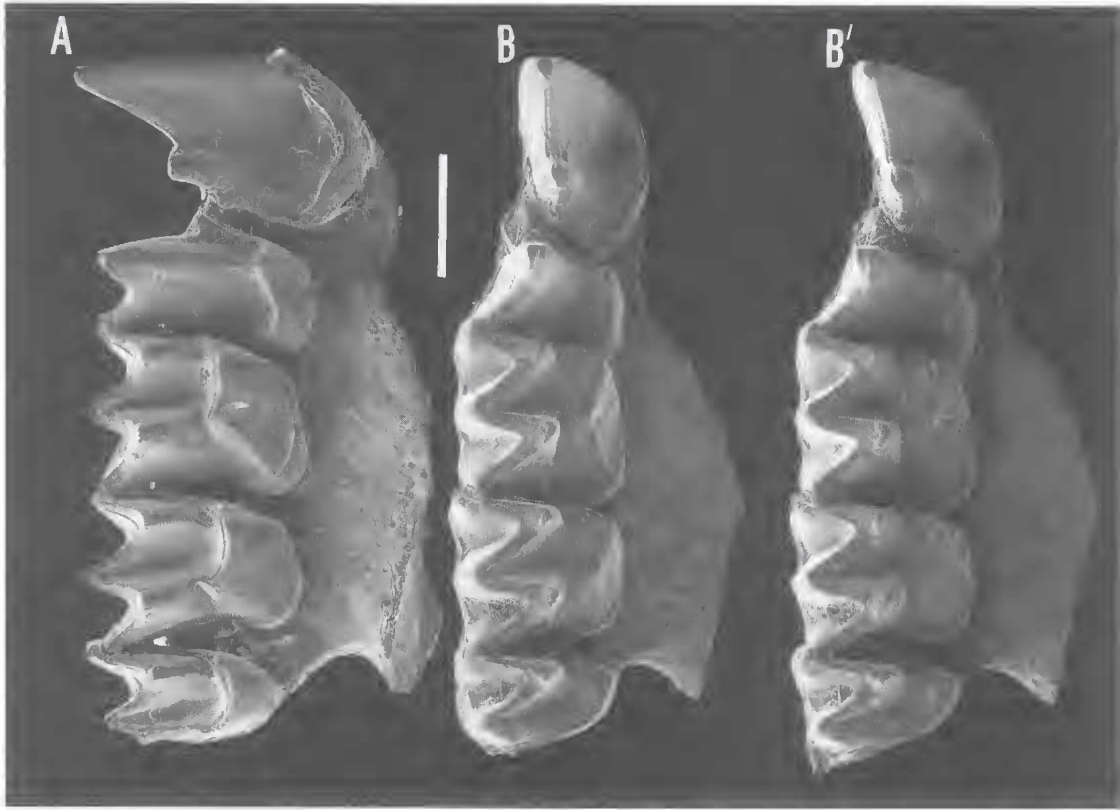


FIG. 2. *Rhinonicteris tedfordi* sp. nov., QMF22912, paratype, maxillary fragment with C¹-M³, from Bitesantennary Site, Riversleigh, northwestern Queensland. A, oblique-occlusal view; B-B', occlusal view, stereopairs. Scale indicates 1 mm.

rior margin of the skull quadrate rather than rounded as in *R. aurantius* and *B. nooraleebus*.

Rostrum distinctly lower than the braincase, more so than in *B. nooraleebus* but less than in *R. aurantius*. Rostral inflations much more prominent than in *B. nooraleebus* and *R. aurantius*, mainly because of the very marked groove leading to a deep frontal depression delimited sharply by well-developed supraorbital ridges. *R. aurantius* with inflations better developed, with very little development of supraorbital ridges, with frontal depression and groove between rostral inflations more limited in depth and extent. Infraorbital foramen wholly above M² as in *B. nooraleebus*, but unlike *R. aurantius* (above M²⁻³), larger and more rounded than in *B. nooraleebus*, smaller and slightly more elongated than in *R. aurantius*. Bar of bone forming its dorsal margin (anteorbital bar; e.g. Hill 1963) straighter and wider anterodorsally than in *R. aurantius* (being roughly the same thickness throughout), (In *R. aurantius* this bone curved, about 3 times as wide

posteroventrally as anterodorsally.), more curved than in *B. nooraleebus*, in which it is roughly the same thickness throughout and very straight. Zygoma (as in *B. nooraleebus* and *R. aurantius*) with an enlarged jugal projection occupying much of its length, as tall as the level of the lower insertion of the anteorbital bar, with slightly convex posterior margin, with its anterior edge posterodorsally directed (rather than vertically).

Sagittal crest well-developed (but see QMF22871), much better developed than in *B. nooraleebus* and different to *R. aurantius*, with maximal height anterior to the middle of the braincase level with the posterior zygomatic roots, not terminating as abruptly nor in a forwardly curving projection as in *R. aurantius*, extending further anteriorly onto the moderately constricted interorbital region, not joining the supraorbital ridges as distinctly as in *B. nooraleebus*, extending posteriorly to the lambdoidal crest, rather than attenuating in the interparietal region as in *R. aurantius*.

TABLE 1. Skull and dental measurements (mm) of type material. H=holotype; P=paratype; two measurements in parentheses in a column indicate (left) and (right), respectively.

	<i>Rhinonictes tedfordi</i>			<i>?Brachiposideros watsoni</i>		
	QMF 22910 (H)	QMF22911 (P)	QMF22912 (P)	QMF22915 (H)	QMF22828 (P)	QMF22916 (P)
Greatest skull length (dorsal)	10.0	15.4		14.4		
Rostral length	5.0	5.5		4.6	24.2	
Braincase length	10.0	9.9		4.6	10.1	
Rostral width (at lacrimal)	5.3	5.2		4.0		
Min. interorbital width	2.5	2.4		4.0		
Zygomatic width	7.5	8.8		7.5		
Mastoid width	(8.9)			7.5	8.3	
Rostral height	4.3	4.0		4.0	4.6	
Braincase height (max.)	7.9	7.2		4.6	7.3	
Palate length	1.6	4.0		1.7	1.5	
Palatal width (base of M ²)	3.0	3.2		2.7	4.6	
Interperiotic distance	1.1	1.5				
C1-M3			5.6			
P4-M3			5.0	(4.1) (4.1)	4.3	
M1-M3			3.5	(3.3) (3.2)	7.5	
C ¹ L			1.1			
C ¹ W			4.0			
P ⁴ L		4.0	1.1	(0.9) (1.0)	3.8	1.1
P ⁴ W		1.1	1.3	(1.0) (0.9)	1.1	1.2
M ¹ L		1.1	1.5	(1.3) (1.3)	1.3	1.1
M ¹ W		2.7	1.1	(1.1) (1.1)	1.5	1.1
M ² L	(1.3) (1.3)	4.3	1.1	(1.2) (1.3)	1.1	8.3
M ² W	(1.4) (1.4)	1.5	1.1	(1.2) (1.2)	1.5	1.4
M ³ L		1.0	0.9	(0.8) (0.9)	0.9	
M ³ W		1.3	1.4	(1.1) (1.2)	1.5	

Premaxillae not known but make a V-shaped junction (often stepped) with the maxillae rather than a rounded V-shape as in *R. aurantius* and *B. nooraleebus*. Palate shorter, with posterior margin extending to the level of the metacone of M² (rather than the anterior face of M³), marked by a short postpalatal spine, as in *R. aurantius*. Mesopterygoid fossa narrow anteriorly, necking in before broadening posteriorly, more similar to *R. aurantius* than *B. nooraleebus* in which it is broad and rounded anteriorly and of uniform width throughout its length.

Lacrimal foramen much larger than in *R. aurantius* and larger than in *B. nooraleebus*. Lateroventral fossa broader than in *R. aurantius* and similar in width to *B. nooraleebus*. Postpalatal and sphenopalatine foramina much larger than in *R. aurantius* or *B. nooraleebus* (QM F19039 but not 19040), closely paired, more distant in *R. aurantius* and well separated in *B. nooraleebus*.

Anterior diploic, ethmoidal and cranio-orbital foramina fused, larger than in *B. nooraleebus*, not fused and large in *R. aurantius*, separated from the optic foramen by a thick bar (rather than broader plate) of bone. Like *R. aurantius*, palate pierced by many foramina, none especially distinctive.

Sphenorbital bridge relatively broad, not greatly constricted posteriorly, with sphenorbital fissure well-exposed. Hammular process very similar to *R. aurantius*, with a conspicuous wing projecting backwards making up at least half its length, with a laterally directed flange of variable length (long in QMF22859) posterior to the hammular process, as in *R. aurantius* and *B. nooraleebus*. Sphenorbital fissure shorter and broader than in *R. aurantius*; optic foramen more lateral than in *R. aurantius*, with the orbitosphenoid splint separating them directed medially rather than posteromedially as in *R. aurantius* and *B. nooraleebus*.

Basisphenoid shallow. Basioccipital width between the periotics as in *R. aurantius* (perhaps slightly narrower), narrower than in *B. nooraleebus*. Postglenoid fossa (?temporal emissary foramen) larger than in *R. aurantius* and *B. nooraleebus*; postglenoid process also slightly better developed than in *R. aurantius*, and much better than in *B. nooraleebus*. Foramen ovale very large; a bar of bone separating the foramen ovale from a ?posteriorly opening fenestra in *B. nooraleebus* is absent in *R. tedfordi* and *R. aurantius* as is the fenestra. The lambdoidal crest is better developed than in *B. nooraleebus*, and in this way more similar to *R. aurantius* (although in the latter this varies intraspecifically e.g. AR 15400 and M8416). Unlike *R. aurantius*, it is continuous across the occipitals in *R. tedfordi* rather than attenuating at the ?nuchal point. Foramen magnum more dorsally oriented than in *B. nooraleebus* and *R. aurantius*, with indentation of its dorsal margin in *R. aurantius* lacking in *R. tedfordi* and *B. nooraleebus*.

Periotic, its orientation and its attachment to surrounding basicranial elements similar to that in *R. aurantius* and *B. nooraleebus*.

Upper teeth approximately the same size in the 3 species, those of *R. aurantius* more hypsodont. Upper incisors unknown. C¹ similar to that in *B. nooraleebus* in width, length and posterior secondary cusp, but with shallower anterolingual cingulum, removing its squared appearance (but see QMF22845). C¹ wider and longer in the tooth row than in *R. aurantius*. P² extruded such that C¹ and P⁴ are in close contact, almost touching (e.g. QMF22845), being closer than in *B. nooraleebus* (although this varies) and at least as close as in *R. aurantius*. P⁴ narrower than in *R. aurantius* (especially anteriorly), the lingual cingulum deeper than in *R. aurantius* and similar to *B. nooraleebus*, and the anterolingual cingular cusp better developed than in *R. aurantius*. M¹ with 4 roots, with heel similar to *R. aurantius* and broader than in *B. nooraleebus*, with a very strong dihedral crest and thickened posterolingual cingulum. Lingual notch incipient, well-developed in QMF22840. M² with 4 roots, evenly spaced, as in *R. aurantius*; *B. nooraleebus* with 3. Its heel much weaker than in *R. aurantius*, similar to *B. nooraleebus* but with the postprotocrista reaching the base of the metacone and with a slight ridge (rather than crest) issuing from its end point (or more anteriorly in worn specimens) and extending to the slightly thickened posterolingual cingulum. M³ similar in the 3 taxa.

COMPARISON. This species differs from the Recent *R. aurantius* in its smaller size, relatively shorter braincase (especially in the postglenoid region), flattened rostral inflations, deep groove between inflations, strong supraorbital ridges, C¹ with less pronounced posterior accessory cusp, P⁴ relatively narrow with greater anterobuccal extension and M² heel much less expanded.

From Riversleigh's *Brachiposideros nooraleebus* Sigé et al., 1982 it differs most conspicuously in its relatively shorter palate with posterior medial spine, its long, slim mesopterygoid fossa, well-developed sagittal and lambdoid crests, more inflated nasals, C¹ without deep anterolingual cingulum, M¹ with broader heel and M² with four roots.

It differs from *B. omani* Sigé, 1995, *B. sp. cf. B. branssatensis* or 'Form X' from St Victor La Coste (Sigé et al., 1982), *B. sp. cf. B. branssatensis* from La Colombière (Sigé et al., 1982) and *B. agulari* Legendre, 1982 in M² having 4 roots. It differs from *B. collongensis* (Depéret, 1892) and *B. dechaseauxi* Sigé, 1968 in the heel of M¹⁻² not being posterobuccally extended and M² invariably having 4 roots. It differs from *B. branssatensis* (Huguency, 1965) in its posterolingual development of the heel of M¹⁻² and generally less conspicuous lingual notch separating protocone from heel in M¹⁻².

Brachiposideros Sigé, 1968

?*Brachiposideros watsoni* sp. nov. (Figs 3-4, Table 1)

ETYMOLOGY. For Neil Watson in recognition of his long association with the University of NSW.

MATERIAL. Holotype QMF22915, skull with LP²-M³ and RP²-M³. Paratypes QMF22828, skull with LC¹-M³ and RP²-M³, QMF22916, maxillary fragment with LC¹-M². Other material QMF22824, QMF22826, QMF22833, QMF22846, QMF22857, QMF22860, QMF22861, QMF22862, QMF22870, QMF22894, QMF22896, QMF22898, QMF22900, QMF22904, QMF22907. All material from the early Miocene Bitesantennary Site (discussed above).

DESCRIPTION. ?*Brachiposideros watsoni* is described in comparison with the Miocene *R. tedfordi* sp. nov., *B. nooraleebus* Sigé et al., 1982 and Recent *R. aurantius* (Gray, 1845).

Skull approximately 10% shorter and narrower than *R. tedfordi*, 20-30% shorter than *R. aurantius*, with braincase length similar to *B. nooraleebus*, with similar overall proportions to *B. nooraleebus* and *R. tedfordi*, rather than *R.*

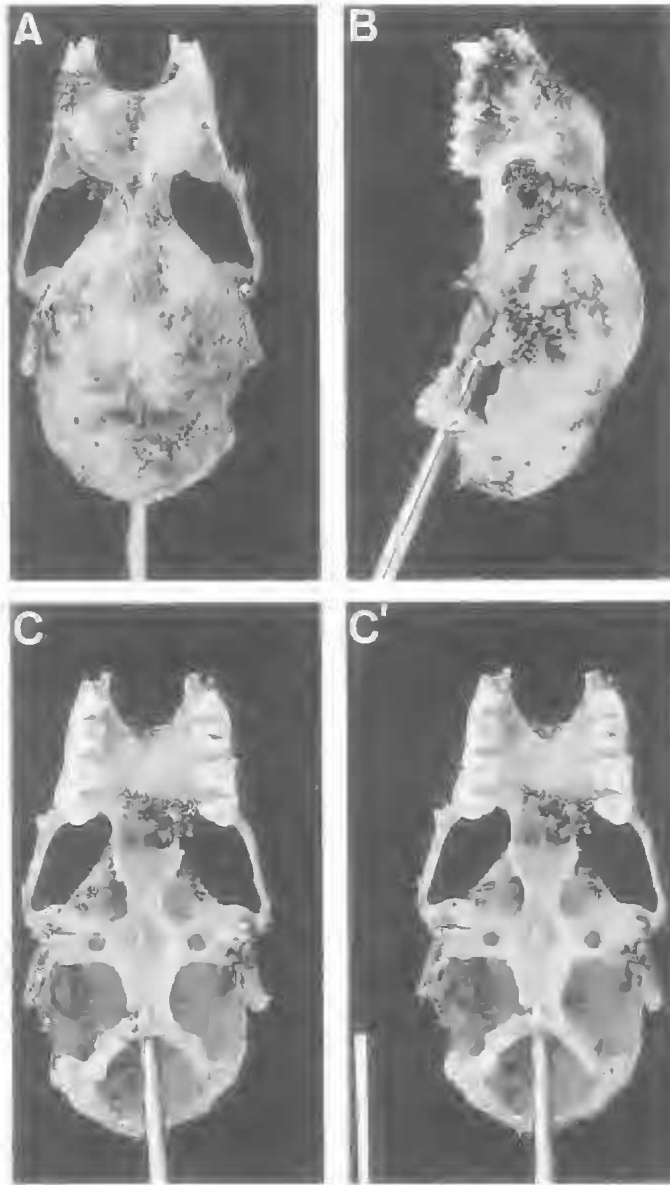


FIG. 3. *Brachipposideros watsoni* sp. nov., QMF22915, holotype, from Bitesantennary Site, Riversleigh, northwestern Queensland. A, dorsal view; B, lateral view; C-C', ventral view, stereopairs. Scale indicates 5 mm.

aurantius (latter much longer in the postglenoid region), with lambdoidal crest generally weaker than in *R. tedfordi*, more like *R. aurantius* and *B.*

nooraleebus, with rounded posterior margin. Sagittal crest lower anteriorly than in *R. tedfordi* and *R. aurantius* but probably slightly taller than in *B. nooraleebus*. As in *B. nooraleebus*, maximal height of braincase more posterior than in *R. tedfordi* and *R. aurantius*, being posterior to the glenoid; sagittal crest remaining tall anteriorly onto the postorbital region (unlike *R. aurantius*), joining the supraorbital ridges fairly distinctly (in QMF22828 supraorbital ridges almost develop wings or flattened plates like an incipient frontal shield), of variable posterior extent (in QMF22915 attenuating in the parietal region, as in *B. nooraleebus* and *R. aurantius*, but in QMF22828 and QMF22843 extending to the lambdoidal crest as in *R. tedfordi*). Zygomatic width greater than mastoid width as in *R. tedfordi* and unlike *R. aurantius*.

Rostrum lower than braincase (not as low as in *R. aurantius* and *R. tedfordi*). Rostral inflations similar in proportion to *R. tedfordi* and *R. aurantius*, more distinct than in *B. nooraleebus*, less distinct than in *R. tedfordi* and *R. aurantius*. Trough between the inflations less pronounced than in *R. tedfordi* but more than in *R. aurantius* and slightly more than in *B. nooraleebus*. Frontal depression shallower than in *R. tedfordi* but deeper than in *R. aurantius* and *B. nooraleebus*, with an unpaired medial frontal foramen. Nasal opening dorsoventrally compressed in anterior view compared to that in *R. tedfordi* and *R. aurantius*; bony nasal septum much longer than in *R. tedfordi* and similar to *R. aurantius*; opening of the vomer sinus round as in *R. aurantius* rather than slit-like as in *R. tedfordi*.

Infraorbital foramen dorsal to M^{2-3} as in *R. aurantius*, rather than M^2 as in *R. tedfordi* and *B. nooraleebus*, more elongate than in *R. tedfordi* and *R. aurantius*. Anteorbital bar slim and generally the same width throughout, as in *B. nooraleebus*, sometimes with a flange or wing, often slightly curved as in *R. tedfordi* and *R. aurantius*. Zygomatic arch with very enlarged jugal projection (QMF22857) extending upwards to at least the level of the upper

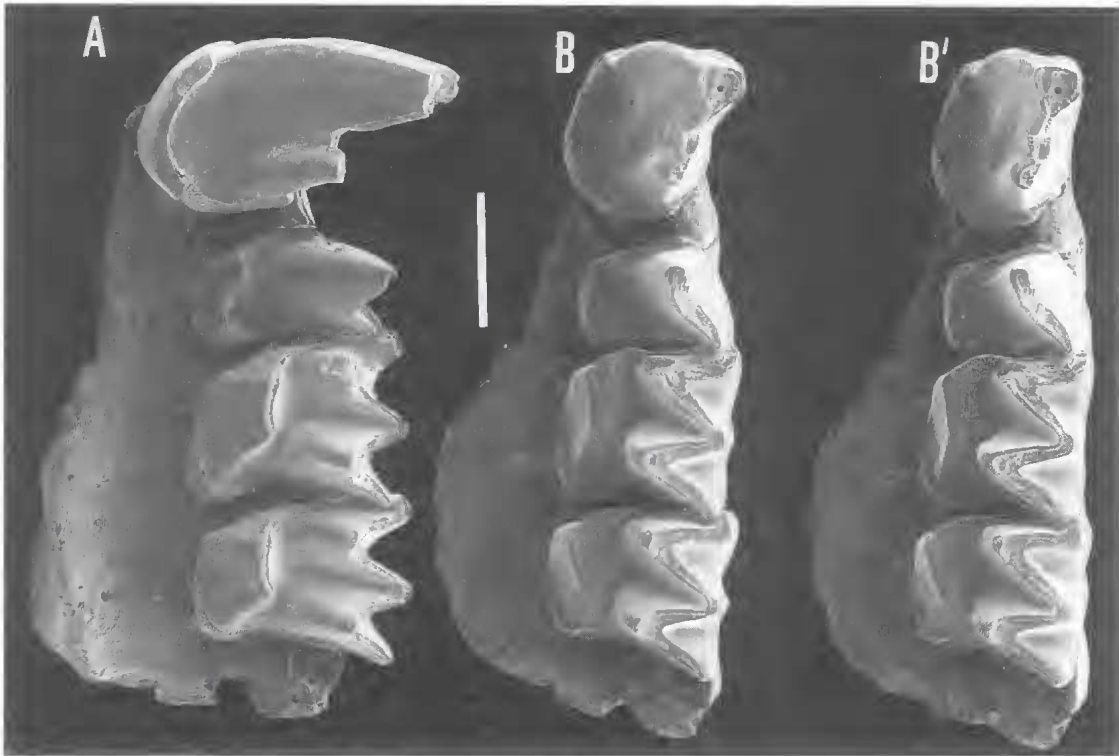


FIG. 4. *?Brachiposideros watsoni* sp. nov., QMF22916, paratype, maxillary fragment with C¹-M², from Bitesantennary Site, Riversleigh, northwestern Queensland. A, oblique-occlusal view; B-B', occlusal view, stereopairs. Scale indicates 1 mm.

insertion of the anteorbital bar, directed slightly posterodorsally, with a rounded but narrow apex, and slightly convex posterior margin.

Premaxillae unknown, with a V-shaped junction to the maxillae as in *R. aurantius*, *B. nooraleebus* and *R. tedfordi*. Palate extending posteriorly to the level of the anterior face of M³ as in *B. nooraleebus* and *R. aurantius*, rather than the M² metacone as in *R. tedfordi*. Bony medial palate spine absent, unlike *R. aurantius* and *R. tedfordi* (variable in *B. nooraleebus*). Mesopterygoid fossa more like that in *B. nooraleebus* than in *R. tedfordi* or *R. aurantius*, being broad and rounded anteriorly and uniform in width throughout its length.

Lateroventral fossa narrower than in *R. tedfordi*, broader than in *R. aurantius* and similar in width to that in *B. nooraleebus*. Lacrimal and postpalatal foramina similar to those in *B. nooraleebus* and smaller than in *R. tedfordi*. Lacrimal larger than in *R. aurantius*; postpalatal foramen and sphenopalatine similar in size to *R. aurantius* (but proportionately larger), approximately equidistant from each other and the three

interorbital foramina (cranio-orbital, ethmoidal and frontal diploic), closely paired with the interorbital foramina more distant in *R. tedfordi*, with intermediate condition in *R. aurantius*, with the sphenopalatine not 'confluent' (i.e. 2 small foramina (QMF19038, QMF19039), and the 3 approximately equidistant) in *B. nooraleebus*. Orbitosphenoid splint separating the optic foramen from the sphenorbital fissure, directed posteromedially like in *B. nooraleebus* and *R. aurantius*, rather than medially as in *R. tedfordi*.

Sphenorbital bridge slightly more constricted posteriorly (posterior to pterygoid processes) than in *R. tedfordi* and *R. aurantius*. Pterygoid wings directed dorsally rather than posteriorly, resulting in shorter wings than in *R. tedfordi* and slightly shorter than in *R. aurantius* (proportionately). Postglenoid fossa slightly smaller than in *R. tedfordi*, but slightly bigger than in *R. aurantius*. Postglenoid process similar to *R. aurantius* and *R. tedfordi* and better developed than in *B. nooraleebus*. Foramen ovale similar to the other taxa; a posteriorly directed fossa relatively smaller than in *R. tedfordi* without bar. Inter-

periotic distance similar to that in *R. tedfordi*. Periotic morphology and orientation and attachment to the basicranium similar to other 3 taxa. Foramen magnum similar to that in *R. tedfordi*, directed more ventrally, as in *R. aurantius* and *B. nooraleebus*.

Teeth smaller than in *R. aurantius* and *R. tedfordi*, approximately same size as in *B. nooraleebus*. Upper incisors unknown. C^1 proportionately shorter (in the tooth row) than in *R. tedfordi* and probably *B. nooraleebus*, more similar to *R. aurantius*. C^1 cingulum not developed as in *R. tedfordi* and *B. nooraleebus*, more like in *R. aurantius*: anterolingual cingulum following the tooth outline rather than thickening in the anterolingual corner. Posterior secondary cusp similar to that in *R. tedfordi* but perhaps taller (in buccal view, $1/3$ to $1/2$ C^1 length rather than $1/3$ in *B. nooraleebus* and *R. tedfordi*). P^2 small and buccally extruded; C^1 and P^4 generally not in contact (but see QM F22907), generally closer, but not in contact in *R. tedfordi* and *R. aurantius*. P^4 narrower than in *R. aurantius* and *B. nooraleebus*, most similar to *R. tedfordi*. M^1 has 4 roots, with heel longer than in *B. nooraleebus*, more similar to *R. tedfordi* and *R. aurantius*. M^2 with 3 roots, like *B. nooraleebus* and unlike *R. tedfordi* and *R. aurantius*, with heel more expanded than in *R. tedfordi*, similar to *B. nooraleebus*, much less expanded than in *R. aurantius*. (Buccal and lingual lengths similar in ?*B. watsoni* and *R. tedfordi*; buccal length greater than lingual length in *B. nooraleebus*.) M^{1-2} crest and cingular development and M^3 similar in the 4 taxa.

COMPARISON. It differs from *R. tedfordi* in its slightly smaller size, shorter mesopterygoid fossa, less anteriorly inflated braincase, more elongate infraorbital foramen, lack of postpalatal spine and M^2 with three roots.

It differs from the Recent *R. aurantius* in its smaller size, much less anteriorly inflated braincase and pronounced sagittal crest, relatively shorter braincase (especially in postglenoid region), flattened rostral inflations, deeper groove between inflations, strong supraorbital ridges, less pronounced accessory cusp on C^1 , P^2 larger and less extruded from the toothrow, P^3 relatively narrow with greater anterobuccal extension and M^2 heel much less expanded and having three roots.

It differs from *B. nooraleebus* in its C^1 lingual cingulum being uniformly shallow, its narrower and shorter P^4 , more expanded M^2 heel, sharp rise in braincase height above glenoid, position of

infraorbital foramen, deep frontal depression and more pronounced supraorbital crests.

It differs from *Brachipposideros branssatensis*, *B. collongensis* and *B. dechaseauxi* in M^2 invariably having three roots. It differs from *B. omani* in its larger size and better developed heel in M^2 . It differs from 'Form X' in its more expanded heel in M^2 . It differs from *B. sp. cf. B. branssatensis* in its posterolingual development of the heels of M^{1-2} and pronounced crests on the posterior flank of the protocone. It differs from *B. aguilaris* in M^1 having four roots.

COMPARISONS OF THE NEW HIPPOSIDERIDS WITH RELATED TAXA

These new species are similar in skull and dental morphology to northern Australia's living *Rhinonictis aurantius* and Microsita's *Brachipposideros nooraleebus* in proportions of the skull, broad rostrum, subparallel tooth rows, palate and zygomatic arch, crested premaxillae, basicranial, periotic and otic morphology, pronounced accessory cusp on C^1 and little reduced upper and lower $M3s$.

Sigé et al. (1982) recognised *R. aurantius* as a probable descendant of the Australian *Brachipposideros* lineage. *Brachipposideros* is known from the Tertiary of Europe, Arabia and Australia (Sigé, 1968; Sigé et al., 1982; Legendre, 1982; Ziegler, 1993; Sigé et al., 1995). The new Riversleigh species can be compared with European and North African taxa only on their upper dentition because: 1) skull material has not been described for non-Australian taxa and 2) dentaries cannot be positively referred to the Riversleigh taxa.

A combination of dental characters is shared by *Brachipposideros* and the new Australian taxa: small size, P^2 between C^1 and P^4 near or on buccal margin of tooth row, C^1 with secondary cusp, P^4 slender with respect to other teeth, M^1 with four roots (loss in some), M^2 with three roots (advanced forms have four), heel of M^1 separated from protocone by a notch (loss secondary) and forming a posteriorly directed lobe. M^2 heel relatively weakly developed, primitively, postprotocrista has prominent anterior portion and only incipiently developed posterior part. *Brachipposideros nooraleebus* shares with European *Brachipposideros* a small lower canine, low coronoid process and similar shape of ascending ramus (Sigé et al. 1982).

The 3 Australian Miocene species differ from the early Oligocene *B. omani* (Sigé et al., 1995)

in their larger size, more recurved C^1 with better developed secondary posterior cusp, and M^2 protocone with weaker dihedral crest. Additionally, *R. tedfordi* differs from *B. omani* in its 4-rooted M^2 .

Compared with *B. sp. cf. B. branssatensis* or 'Form X' (Sigé et al. 1982) of the French late Oligocene (Chattian), the Australian species have P^2 smaller and further extruded from the toothrow, P^4 with better developed anterolingual cingular cusp, P^4 wider with respect to M^{1-2} (closest to ?*B. watsoni*), M^{1-2} heels more posterolingually developed and posteriorly directed, M^2 heel more expanded with dihedral crest and posterolingual cingulum stronger in Australian taxa. M^3 size is similar.

The early Miocene (Lower Aquitanian) French species *B. branssatensis* (Hugueney, 1965) has quite different M^{1-2} heel development from Australian species, with heel expansion occurring at the posterolingual corner but directed buccally, and having a pronounced lingual notch, a variable characteristic in Australian taxa. The M^2 heel is better developed than in Australian forms but the dihedral crest is more pronounced in Australian taxa as is (probably) the posterolingual cingulum. C^1 is similar to that in ?*B. watsoni* and *R. tedfordi*, in which the lingual cingulum is uniform and follows the curvature of the tooth, and hence unlike *B. nooraleebus*. P^2 position and size are similar but in Australian forms P^2 is generally smaller and more extruded. The infraorbital foramen occurs dorsal to M^2 as in *R. tedfordi* and *B. nooraleebus*.

M^{1-2} heel expansion in the Australian taxa is more similar to that found in the French early Miocene (Lower Aquitanian) *B. sp. cf. B. branssatensis* from La Colombière, in direction of expansion and strong crest on the posterior flank of the protocone, C^1 is smaller in size and the lingual cingulum uniform and even in depth, but with similar thickening in its anterolingual corner as in *R. tedfordi*. The posterior margin of P^4 is very curved, the anterior margin narrower and the anterobuccal extension greater than in ?*B. watsoni* and similar to *B. nooraleebus*. M^1 , and M^2 ?variably, has 4 roots.

The French early to early middle Miocene (Upper Aquitanian) *B. dechaseauxi* Sigé, 1968 is larger than the Australian species. The posterior flank on the M^{1-2} protocone is simply rounded with the dihedral crest poorly developed, the heel is directed posteriorly to posterobuccally like *B. branssatensis*. M^{1-2} width is very similar to that of M^3 , ?variably developed lingual notch separat-

ing protocone and heel. P^4 is narrow with respect to M^{1-3} , possibly smaller than in ?*B. watsoni*, its anterobuccal extension much greater than in Australian taxa. P^2 is outside the toothrow, but is probably similar to Australian taxa in size and position. C^1 has a uniform lingual cingulum as in ?*B. watsoni* and *R. tedfordi*.

M^{1-2} heel development in the French early to early middle Miocene (Burdigalian) *B. aguilari* Legendre, 1982 is sharper than the Australian species but the direction of expansion and crest on the protocone are similar. The posterolingual heel cingulum is not well-developed. The crest is continuous with the posterior lingual cingulum in *B. aguilari*. In M^{1-2} the ectoloph is different: the buccal edge is angular rather than rounded as in the Australian taxa. P^4 appears to be relatively large and C^1 gracile with a uniformly deep lingual cingulum like ?*B. watsoni*.

The type species, *B. collongensis* (Depéret, 1892), from the French early middle Miocene (Upper Burdigalian) is similar in size to *B. watsoni* and *B. nooraleebus* but P^2 is less extruded from the toothrow, M^{1-2} heels posterobuccally developed like *B. branssatensis* and *B. dechaseauxi* and M^2 heel better developed but with weaker dihedral crest especially in M^2 whose protocone flank is rounded. P^4 is relatively wide with respect to M^{1-3} as in the Australian species.

PHYLOGENETIC RELATIONSHIPS

On dental characters, the new Australian species are more similar to each other and to *B. nooraleebus* than to non-Australian taxa. Sigé et al. (1982, figs 8-9) found that compared to European species, the dental structure of *B. nooraleebus* was more advanced than Aquitanian forms and as advanced as Burdigalian species. The Chattian 'Form X' was considered close to the base of the European radiation, with *B. branssatensis* close to the group that gave rise to the *B. collongensis* and *B. dechaseauxi* lineages and *B. sp. cf. B. branssatensis* closer to *B. aguilari* and *B. nooraleebus*. Apomorphies shared by *B. sp. cf. B. branssatensis*, *B. aguilari* and *B. nooraleebus* included heel of M^{1-2} separated from the protocone by a slight lingual notch and heels developed posterolingually and directed posteriorly. *Brachiposideros aguilari* and *B. nooraleebus* share further reduction of P^2 so that C^1 and P^3 are close and sometimes in contact, P^4 relatively larger and M^{1-2} protocone with pronounced dihedral crest.

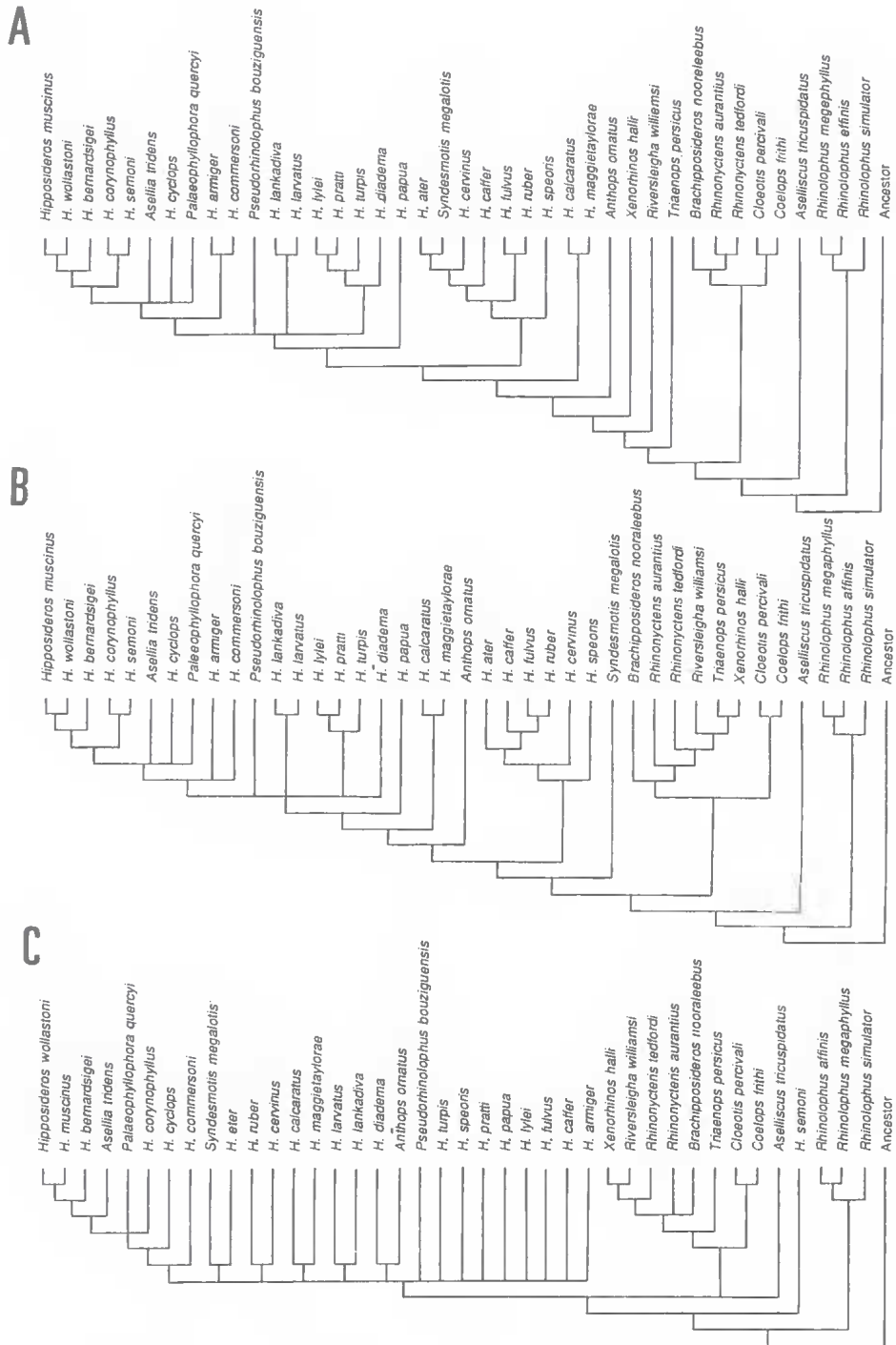


FIG. 5. Phylogenetic hypotheses of hipposiderid relationships presented by Hand & Kirsch (in press) resulting from analyses conducted on 40 taxa and 59 dental, cranial and skeletal characters: A, Strict consensus of 4 PAUP trees, all unordered characters (CI=0.25; 87.5% resolution); B, Strict consensus of 8 PAUP trees, some ordered characters (CI=0.23; 82.5% resolution). C, Hennig86 Nelson consensus, unordered characters. See Hand & Kirsch (in press) for characters and character states.

TABLE 2. Distribution of character-states used in a phylogenetic analysis of relationships among *Brachipposideros* and *Rhinonictoris* species, and related taxa, based on dental characters only. 0=interpreted plesiomorphic condition, 1-3=apomorphic states, ?=missing data or character does not apply.

Taxon	Character states
<i>B. omani</i>	?1?? ???? 01 ?11
<i>B. brassatensis</i>	100? 0011 01 011
<i>B. sp. cf. B. branssatensis</i>	1000 0011 01 011
<i>B. collongensis</i>	1011 0101 11 011
<i>B. aguilari</i>	1012 1122 01 011
<i>B. dechaseauxi</i>	1010 0011 11 011
<i>B. nooraleebus</i>	1002 0022 01 011
? <i>B. watsoni</i>	1001 0022 01 011
<i>R. tedfordi</i>	1012 0022 11 011
<i>R. aurantius</i>	1012 0122 12 011
<i>Hipposideros ater</i>	0201 ?022 01 111
<i>Anthops ornaus</i>	0100 ?021 ?0 100
Ancestor	0000 0000 00 000

Characters:

- 1: Height of ascending ramus of dentary: 0=tall, 1=low
- 2: C¹ accessory cusp: 0=present, 1=poorly developed, 1=absent
- 3: P² extrusion: 0=extruded but still separating C¹ and P⁴, 1=C¹ and P⁴ in contact or nearly so
- 4: P⁴ width wrt other cheekteeth: 0=narrow, 1=medium, 2=wide
- 5: M¹ no. of roots: 0=4, 1=3
- 6: M¹ heel development/length: 0=moderate, 1=strong
- 7: M¹ heel direction: 0=none, 1=posterobuccal, 2=posterolingual
- 8: M¹ lingual notch: 0=absent, 1=inconspicuous, 2=conspicuous
- 9: M¹ dihedral crest: 0=absent, 1=weak/medium, 2=strong
- 10: M² number of roots: 0=3, 1=4
- 11: M² heel length/development: 0=none, 1=slight, 2=great
- 12: M² heel direction: 0=none, 1=posterobuccal, 2=posterolingual
- 13: M² dihedral crest: 0=absent, 1=weak/medium, 2=strong

The new Bitesantennary species also share these apparent apomorphies and are assigned to that clade. Although *tedfordi* shares with the *B. branssatensis*, *B. collongensis* and *B. dechaseauxi* lineages a fourth root on M² it does not share the distinctive posterobuccally expanded heels on M¹⁻². In this case a four-rooted M² is interpreted to be homoplastic; it occurs also in *R. aurantius*.

A phylogenetic analysis of the interrelationships of 12 hipposiderid species including 10

species of *Brachipposideros* and an hypothetical ancestor, based only on dental features (13 characters) (Table 2) and using the clustering program PAUP 3.1.1 (Swofford 1993), was unable to resolve relationships within the group (percent resolution of trees 18.2%). Tree resolution did not improve when the most poorly known species, *B. omani*, was removed, nor if character states were ordered. However, majority rule trees (50%) did show the European *B. branssatensis*, *B. dechaseauxi* and *B. sp. cf. B. branssatensis* (Form X) clustering in 67% of trees, as did *B. collongensis*, *B. aguilari*, *R. tedfordi* and *R. aurantius*. Hand & Kirsch (in press) found in their phylogenetic analyses of 37 hipposiderids that dental features (20 characters) were not sufficient to interpret relationships among genera and species groups of the Hipposideridae. They found that resolution of trees was less than 33% when dental features only were used, compared with 87.5% resolution with a combined data set of cranial, dental and skeletal characters.

Brachipposideros Sigé, 1968 was erected as a subgenus of *Hipposideros* Gray, 1831. However, probable patristic relationships between *Brachipposideros* and *Rhinonictoris*, indicate that the evolutionary relationships of these taxa are not adequately reflected by current taxonomy. Hand & Kirsch (in press) found *Hipposideros* to be almost certainly paraphyletic, as did Bogdanowicz & Owen (in press). Huguency (1965), Sigé (1968) and Legendre (1982) all suggested that *Hipposideros* was paraphyletic.

Hand & Kirsch (in press) also found that *B. nooraleebus* was more closely related to *Rhinonictoris* (*aurantius* and *tedfordi*), and possibly other Australian Miocene hipposiderids than to *Hipposideros* (Fig. 5A-C). Because that analysis was based on cranial as well as dental characters, European *Brachipposideros* taxa could not be included, and precise relationships between non-Australian and Australian *Brachipposideros* species remain unclear.

Relationships between *Brachipposideros*, *Rhinonictoris* and other Australian Miocene hipposiderids were not completely resolved in the analyses by Hand & Kirsch (in press). However, in all trees *nooraleebus* occurred as the plesiomorphic sister-species to a clade consisting of, or containing, *aurantius* and *tedfordi*. In some trees, *aurantius* and *tedfordi* formed part of a broader group of Australian Miocene hipposiderids including *Xenorhinos* and *Riversleigh* (Fig. 5B-C).

When *watsoni* was included in PAUP analyses

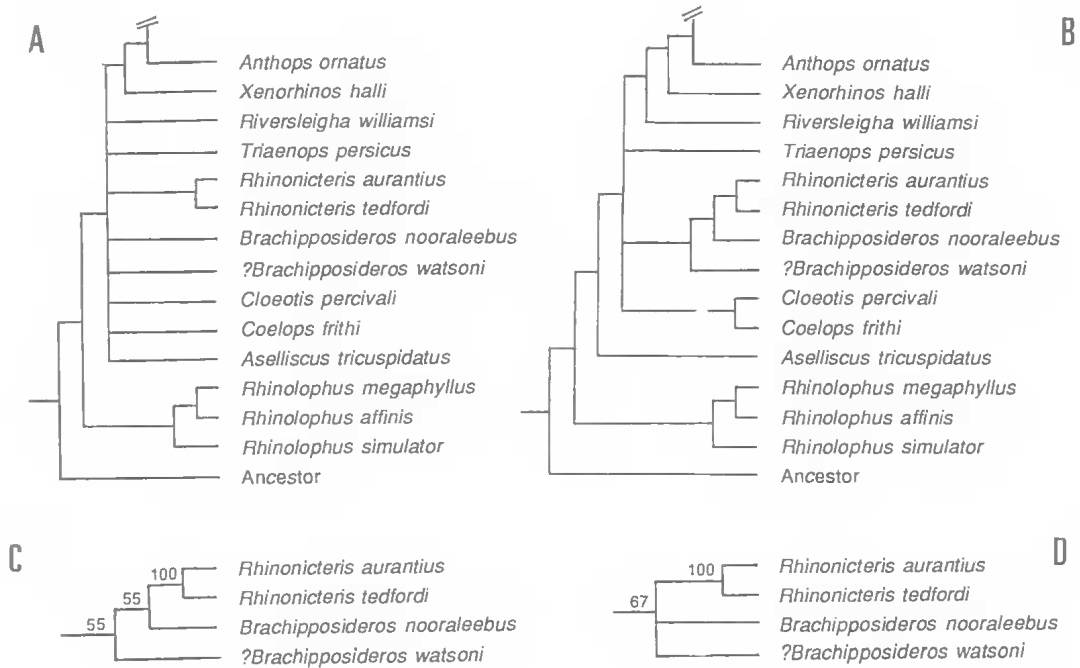


FIG. 6. Phylogenetic hypotheses of relationships of 40 hipposiderids plus *?Brachipposideros watsoni* resulting from PAUP analyses conducted on 59 characters (Hand & Kirsch, in press). A, Strict consensus of 44 trees (CI=0.24; 55% percent resolution), all unordered; B, 50% majority rule tree of 6A; C, D, % support (majority rule) for clustering of *Rhinonicterus* and *Brachipposideros* taxa, trees based on unordered and ordered characters respectively.

of the same taxa and characters used by Hand & Kirsch (in press), resolution of relationships between hipposiderid taxa fell (from over 82% to less than 60% in all analyses). Relationships among crown groups (i.e. *Hipposideros*, *Asellia*, *Palaeophyllophora* and *Pseudorhinolophus*) remained unchanged from those shown in Fig. 5 (indicated by broken line in Fig. 6A-B), but resolution at the base of the trees (e.g., among *Brachipposideros*, *Rhinonicterus*, *Coelops* and *Cloeotis*) decreased markedly (cf. Figs 5A and 6A). Majority rule trees (50%) clustered species of *Rhinonicterus* and *Brachipposideros* (e.g., Fig. 6B), but with little consensus on relationships between *watsoni*, *nooraleebus* and an *aurantius*-*tedfordi* clade (Fig. 6C-D).

On the basis of all analyses (Hand & Kirsch in press and herein), *watsoni* and *tedfordi* are assigned to a clade also containing *B. nooraleebus* and *R. aurantius*. However, the interrelationships

between these taxa is not as clear. Skull morphology of *nooraleebus* (e.g., its poorly developed sagittal crest, shallow frontal depression and poorly inflated nasals) is less derived than that of *watsoni*, but its dentition (e.g., large P^4) would exclude it from being a structural ancestor to *watsoni*. Here, *watsoni* has been tentatively assigned to *Brachipposideros*, and *tedfordi* to *Rhinonicterus*. *Brachipposideros nooraleebus* is known from fragmentary material with key features of the sphenorbital bridge area lacking (Hand, 1993, fig.1). However, both *nooraleebus* and *watsoni* lack a number of apparent apomorphies shared by *tedfordi* and *aurantius*, including an anteriorly vaulted braincase and low but conspicuously inflated rostrum, a round infraorbital foramen bordered by a curved anteorbital bar, a postpalatal spine, a narrow, scalloped mesopterygoid fossa, a poorly (posteriorly) constricted sphenorbital bridge with long (an-

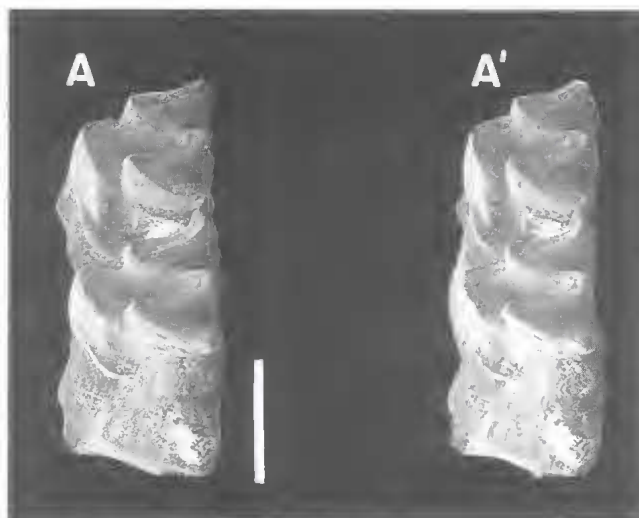


FIG. 7. ?*Brachipposideros* sp., QMF22917, maxillary fragment with M^{1-2} , from Upper Site, Riversleigh, northwestern Queensland. A-A', stereopairs, oblique-occlusal view. Scale indicates 1 mm.

teroposteriorly) pterygoid wings, and M^2 with four (rather than three) roots. Fewer apomorphies appear to be shared between *watsoni* and *nooraleebus*, but potentially include the posterior extension of the supraorbital crest and elongated infraorbital foramen.

Recent *R. aurantius* can be distinguished from the Miocene *R. tedfordi* by its larger size, relatively longer braincase (especially in postglenoid region), little or no groove between inflations, weaker supraorbital ridges, more expanded heel on M^2 , more pronounced accessory cusp on C^1 , P^4 relatively wide with little anterobuccal extension, and P^2 small and further extruded. In Riversleigh's Pliocene Rackham's Roost deposit, an early population of *R. aurantius* occurs syntopically with other as yet undescribed *Rhinonictoris* and/or *Brachipposideros* species, and today *R. aurantius* is still found in the general area.

DISCUSSION

I raise *Brachipposideros* Sigé, 1968 from subgeneric to generic level. Tentatively, it would include non-Australian species *B. branssatensis*, *B. collongensis*, *B. dechaseauxi*, *B. omani*, *B. aguilari* and *B. sp. cf. B. branssatensis* as well the Australian Miocene species, *nooraleebus* and *watsoni*. Although this may be a paraphyletic group, evidence is conflicting and relationships between Australian and non-Australian taxa are

difficult to determine on dental morphology alone. Until further information becomes available, all non-Australian and the least derived Australian taxa (i.e., those lacking obvious synapomorphies for *Rhinonictoris*) are referred to *Brachipposideros* as perhaps the simplest, if not entirely accurate, reflection of the group's evolutionary relationships.

?*Brachipposideros* sp. (Fig. 7), a maxillary fragment of a Miocene hipposiderid from Riversleigh's Upper Site, preserves M^1 and M^2 which are strikingly similar to those of the *B. collongensis* and *B. branssatensis* lineages, particularly in their posterobuccally-directed heel development which is quite unlike any other known Riversleigh hipposiderid.

The Bitesantennary Site is a Miocene cave-fill in which ?*B. watsoni* and *R. tedfordi* occur with at least 8 other hipposiderids, 5 of which are yet to be described. Five of the 10 Bitesantennary hipposiderids, including ?*B. watsoni* and *R.*

tedfordi, are well represented, each by tens or hundreds of complete skulls; the other 5 hipposiderids, and a megadermatid (cf. *Macroderma godthelpi*), are represented by fewer, more fragmentary specimens. The generally very fine preservation of the remains (often with periotics in situ) suggests that fossilisation occurred quickly with little transport, probably in still water rather than guano (in which biodegradation would be expected). Few juvenile bats are among among the thousands represented, suggesting that this cave (or part thereof) was not used as a maternity roost.

By analogy with modern bat communities, the high diversity of hipposiderids in the Bitesantennary deposit suggests warm, humid conditions in the cave, and probably outside it. In Europe, appearance of *Brachipposideros* in the fossil record coincides with a period of steadily increasing temperature and their disappearance probably correlates with the climatic deterioration across Europe in the later Pliocene (Aguilar et al., in press). In Australia, 6 hipposiderids are restricted to northern tropical areas. *Rhinonictoris aurantius* roosts in very warm, humid caves in colonies of 20 to several thousand individuals from NW Queensland to NW WA. It emerges at dusk to feed, mostly on moths but also on beetles, shield-bugs, parasitic wasps, ants, chafers and weevils (Jolly & Hand, 1995). Although *R. aurantius* and the Miocene *Rhinonictoris tedfordi*

are closely related and similar in many skull features, the extinct species lacks the forward-projecting development of the sagittal crest that characterises *R. aurantius*, and it is unclear whether or not they could be described as ecological vicars.

Hipposiderid bats promise to be useful biostratigraphic indicators in the limestones at Riversleigh. They are the most common bats in Riversleigh's Miocene deposits, the best preserved, and, with megadermatids, currently the best understood in terms of their phylogenetic relationships as well as their morphological variability (Sigé et al., 1982; Hand, 1993, 1995, 1997). *Brachhipposideros nooraleebus* is known only from Microsite and ?*B. watsoni* only from Bitesantennary Site. *Rhinonictis tedfordi*, however, is known from Bitesantennary Site in the Verdon Creek Sequence, RV and Upper Sites on Godthelp's Hill, and White Hunter Site on Hal's Hill. None of the species described herein has been recorded from System C sites (Archer et al., 1989, 1994; Creaser, this volume), but close relatives (?descendants) occur at sites such as Gotham City and Dome North Sites suggesting that lineages may be identified within the Riversleigh limestone sequence.

ACKNOWLEDGEMENTS

Work at Riversleigh has been supported by the Australian Research Council, the Department of the Environment, Sport and Territories, National Estate Programme Grants (Queensland), Queensland National Parks and Wildlife Service, the Australian Geographic Society, the Linnean Society of New South Wales, ICI, the Queensland Museum and the University of NSW. I thank Michael Archer, Henk Godthelp and Bernard Sigé for their help and encouragement and two referees for constructive criticism of this paper. Skull photographs are by Ross Arnett and Robyn Murphy, University of NSW.

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